

Integrative revision of the *Caryocolum schleichi* species group – a striking example of a temporally changing species concept (Lepidoptera, Gelechiidae)

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<http://zoobank.org/D9502F1A-AEC0-4B0F-845C-87D86632AF17>

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Academic editor: Bernard Landry ♦ Received 31 January 2020 ♦ Accepted 24 March 2020 ♦ Published 23 April 2020

Abstract

The taxonomy of the Palaearctic *Caryocolum schleichi* species group is revised, leading to a largely new species concept. Initially described as four different species (*C. schleichi*, *C. arenariella*, *C. dianthella*, *C. improvisella*), these taxa were later considered as subspecies. Recently the taxon *C. arenariella* was re-instated to species level without, however, revision of the remaining three subspecies. Analysis of DNA barcodes of the mtCOI (Cytochrome c Oxidase 1) gene of all four validly described taxa showed an unexpected pattern of genetic diversity. Careful re-examination of morphological traits, particularly male and female genitalia, fully supported this pattern, leading to the re-instatement of *C. dianthella* **sp. rev.** and *C. improvisella* **sp. rev.** as valid species and the description of three new species, all of them occurring in the Alps: *C. messneri* **sp. nov.** (Italy, Slovenia, Bulgaria, Greece), *C. lamai* **sp. nov.** (Italy, France) and *C. habeleri* **sp. nov.** (France, Switzerland, Germany). All species are described in detail and the adults and genitalia of both sexes are illustrated.

Key Words

cryptic diversity, new species, integrative taxonomy, DNA barcode, morphology, Alps

Introduction

With about 865 species the Gelechiidae are among the most diverse families of Lepidoptera in Europe, only exceeded by the Tortricidae, Geometridae and Noctuidae. Additionally, many undescribed species probably exist (Huemer and Karsholt 2020) and it seems not unlikely that the species number will rise to 1000. In contrast to several unrevised groups of Gelechiidae, the genus *Caryocolum* has received above-average attention with extensive revisionary work on a continental or inter-continental scale (Klimesch 1953–1954; Huemer 1988; Huemer and Karsholt 2010). Collecting efforts in remote areas and the introduction of molecular traits has further contributed to an increase of previously overlooked diversity and the number of described species has reached

57 in Europe (Bella 2008; Grange and Nel 2012; Huemer and Nel 2005; Huemer and Karsholt 2010; Huemer et al. 2014; Nel and Requena 2017; Huemer and Karsholt 2020). However, Huemer et al. (2014) from extensive DNA barcoding of a large portion of the European fauna have already indicated several species groups with potentially cryptic species. One of these groups is that of *Caryocolum schleichi* s.l., revised in this paper. Following the taxonomic revision of *Caryocolum* (Huemer 1988) this species was considered as a morphologically variable taxon with several geographically separated subspecies in Europe and parts of Asia: *C. schleichi schleichi* (Christoph, 1872), *C. schleichi dianthella* (Chrétien, 1925), *C. schleichi improvisella* (Rebel, 1936) and *C. schleichi arenariella* (Benander, 1937), all of them initially described as species. However, Aarvik et al. (2017),

without in-depth discussion, re-instated *C. arenariella* as a separate species, leaving the remaining taxa untouched. Extensive studies of barcode sequences of the mitochondrial COI gene (Huemer et al. 2014) had already indicated species level for this species and the remaining subspecies and the possibility of further cryptic species. These shortcomings are here formally resolved with two subspecies reinstated to species level and the unexpected discovery of three hitherto unnamed species.

Material and methods

Generic descriptions of *Caryocolum* have been published by Huemer (1988) and Huemer and Karsholt (2010) and are thus not repeated here.

Specimens

The study is based on about 200 specimens of the *Caryocolum schleichi*-group. Material was either traditionally set and dried or, particularly more recently, mainly spread or only pinned. Genitalia preparations usually followed standard techniques (Robinson 1976) adapted for the male genitalia of Gelechiidae and female genitalia of *Caryocolum* by the “unrolling technique” as described by Pitkin (1986) for males and Huemer (1987) for females.

DNA Barcodes

DNA barcode sequences are based on a 658 base-pair long segment of the mitochondrial COI gene (cytochrome c oxidase 1). DNA samples (dried legs) were prepared according to the prescribed standards. Legs from 33 specimens of the *Caryocolum schleichi* species group were successfully processed at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) to obtain DNA barcodes using the standard high-throughput protocol described in deWaard et al. (2008), supplemented by a further 12 public sequences from BOLD. Sequences were submitted to GenBank, and further details including complete voucher data and images can be accessed in the public dataset “Lepidoptera of Europe – *Caryocolum schleichi* species group [DS-CARYSCHL]” in the Barcode of Life Data Systems (BOLD; Ratnasingham and Hebert 2007). Degrees of intra- and interspecific variation of DNA barcode fragments were calculated under the Kimura 2 parameter model of nucleotide substitution using analytical tools of BOLD systems v. 4.0. (<http://www.boldsystems.org>). A Neighbor-Joining tree of DNA barcode data was constructed using MEGA 6 (Tamura et al. 2013) under the Kimura 2 parameter model for nucleotide substitutions. A three-letter code (ISO 3166-1 alpha-3, https://en.wikipedia.org/wiki/ISO_3166-1_alpha-3) was used to abbreviate country names.

Photographic documentation

Photographs of the adults were taken with an Olympus SZX 10 binocular microscope and an Olympus E 3 digital camera and treated using the software Helicon Focus 4.3, Adobe Photoshop CS4, and Lightroom 2.3 softwares. Genitalia photographs were taken with an Olympus E1 Digital Camera through an Olympus BH2 microscope.

Specimen repositories

BNCH	Bündner Naturmuseum, Chur, Switzerland
LMK	Landesmuseum Kärnten, Klagenfurt, Austria
MMB	Mendel Museum, Brno, Czech Republic
NHM	Natural History Museum, London, United Kingdom
NHMW	Naturhistorisches Museum, Wien, Austria
NMPC	National Museum Prague, Czech Republic
RCJS	Research Collection Jürg Schmid, Illanz, Switzerland
RCGL	Research Collection Gérard Labonne, Montpellier, France
RCPL	Research Collection Peter Lichtmannecker, Adlkofen, Germany
RCRH	Research Collection Richard Heindel, Günzburg, Germany
RCTM	Research Collection Toni Mayr, Feldkirch, Austria
TLMF	Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria
ZCLU	Zoological Collections, University of Lund, Sweden
ZMUC	Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark
ZMUO	Zoological Museum, University of Oulu, Finland
ZSM	Zoologische Staatssammlung, Munich, Germany

Results

Molecular analysis

Successfully sequenced specimens originate mainly from Europe, with a few exceptions of Asian vouchers (Fig. 1). DNA sequencing resulted in a full barcode fragment for 38 specimens, 6 sequences > 600 bp and a single shorter sequence of 568 bp which were considered for analysis. Seven distinct DNA barcode clusters were observed, supporting the already known four taxa (irrespective of subspecies or species level) and another three hitherto unrecorded putative taxa. Subsequent morphological examination of these clusters resulted in a fully concordant pattern of seven morphospecies (see below).

Sequences of the COI barcode region of these morphospecies reveal moderately low intraspecific but significant interspecific genetic distances. Mean distances within species are 0.60% with a minimum of 0% and

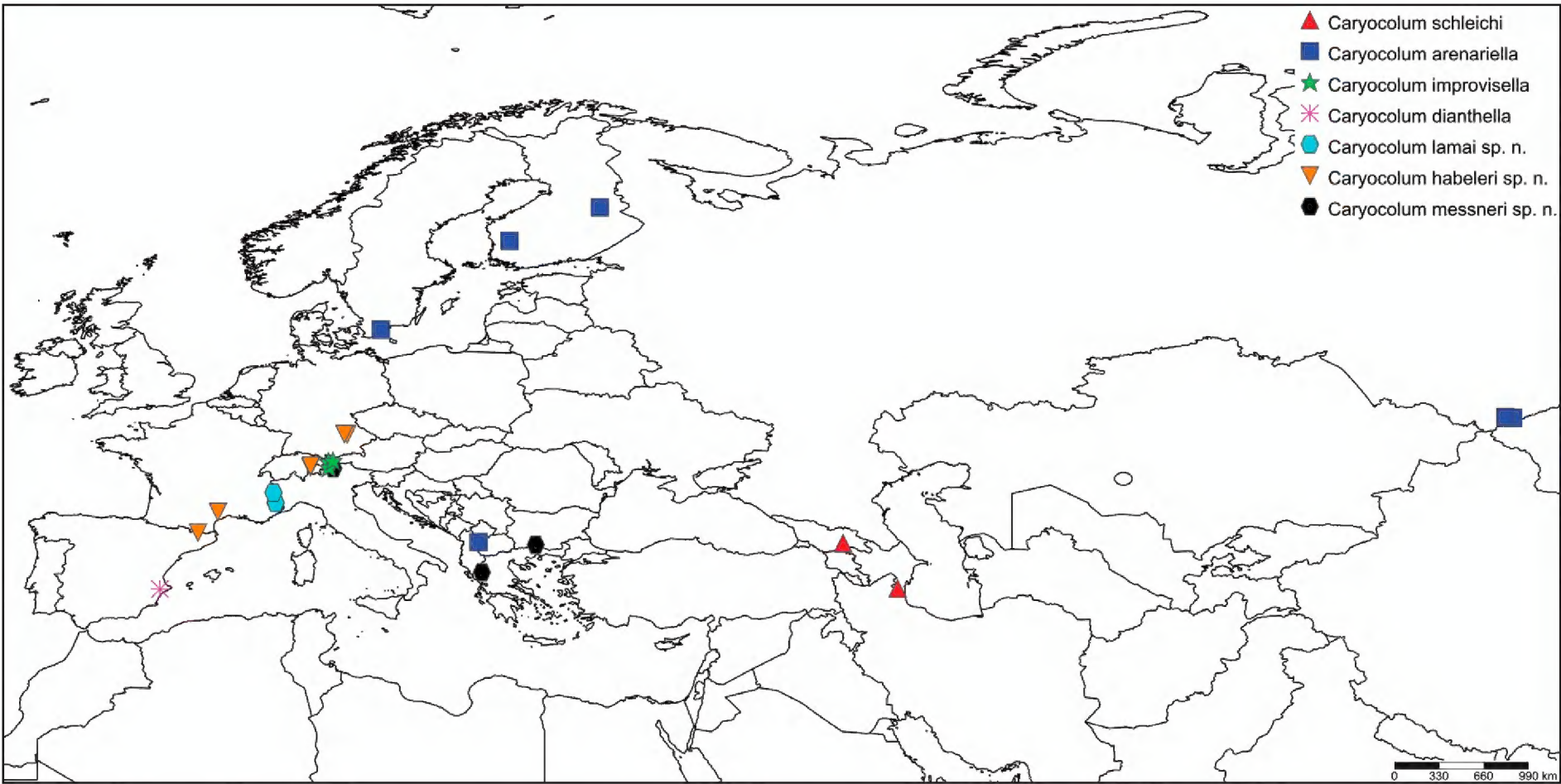


Figure 1. Distribution map of successfully sequenced material of the *C. schleichi* species group. Map created with SimpleMapp (http://www.simplemapp.net).

maximum of 1.71%. Mean interspecific distances are much higher with 4.71%, ranging from minimum 2.35% to maximum 6.47%. Barcode gaps range from 2.35% to 3.43% to the nearest neighbor (Fig. 2, Table 1).

Taxonomic conclusions

Caryocolum Gregor & Povolný, 1954

Caryocolum Gregor and Povolný 1954: 87; Type species: *Gelechia leucomelanella* Zeller 1839: 138.

Caryocolum schleichi species group

The *Caryocolum schleichi* species group belongs to the *leucomelanella*-group as defined by Huemer (1988) and which is characterized in the male genitalia by the strongly sclerotized transtilla, without spines, the broad valva with one or two processes, two pairs of digitate processes at the posterior margin of the vinculum and a straight phallus with minute apical cornuti. In the fe-

male genitalia the group is characterized by the lack of specialized structures of segment VIII, the folds delimiting antrum and joined in medial part of segment VIII, the short antrum and the long lateral sclerotizations in the posterior part of the ductus bursae. The *Caryocolum schleichi* species group itself is characterized by the distally broad valva with two processes, a unique structure in *Caryocolum*.

Larvae of the *Caryocolum schleichi* species group are restricted to the genus *Dianthus* L. (Caryophyllaceae) as far as known.

Checklist

Caryocolum schleichi (Christoph, 1872)
Caryocolum dianthella (Chrétien, 1925) stat. rev.
Caryocolum improvisella (Rebel, 1936) stat. rev.
Caryocolum arenariella (Benander, 1937)
Caryocolum messneri sp. nov.
Caryocolum lamai sp. nov.
Caryocolum habeleri sp. nov.

Key to male genitalia

The key is only based on male genitalia structures. Adults and female genitalia are inseparable in some species.

- 1 Valva with shortly pointed dorso-apical process, 1/5 to 1/8 length of sacculus (Figs 13, 14, 20–22, 28)..... 2
- Valva with long and acute dorso-apical process, 1/3 to 2/3 length of sacculus (Figs 15–19, 23–27)..... 4
- 2 Dorsal edge of valva with distinct sub-apical hump (Figs 14, 22) *C. dianthella*
- Dorsal edge of valva weakly concave, without sub-apical hump (Figs 13, 20–21, 28) 3
- 3 Dorso-apical process of valva basally broad; sacculus slender, about one-third width of valva (Figs 13, 21)..... *C. schleichi*
- Dorso-apical process of valva narrow; sacculus broad, about half width of valva (Figs 20, 28) *C. habeleri*

- 4 Dorso-apical process of valva longer than ventro-apical process, slender, valva with nearly straight outer edge sub-apically; posterior margin of vinculu with pair of short digitate processes (Figs 17, 19, 25, 27)..... 5
- Dorso-apical process of valva shorter than ventro-apical process, slender with distinctly broader base, valva with weakly concave outer edge subapically; posterior margin of vinculum with pair of long digitate processes (Figs 15, 16, 18, 23, 24, 26) 6
- 5 Sacculus slender, 4 times longer than maximum width; medial process of vinculum moderately short, extending to posterior third of lateral process (Figs 17, 25)..... *C. arenariella*
- Sacculus very slender, about 5 times longer than maximum width; medial process of vinculum short, extending to middle of lateral process (Figs 19, 27)..... *C. lamai*
- 6 Valva broad, distally weakly dilated; latero-medial processes of the vinculum hump-like, broader than long (Figs 15, 16, 23, 24) *C. improvisella*
- Valva moderately slender, with parallel outer edges; latero-medial processes of the vinculum digitate, distinctly longer than broad (Figs 18, 26) *C. messneri*

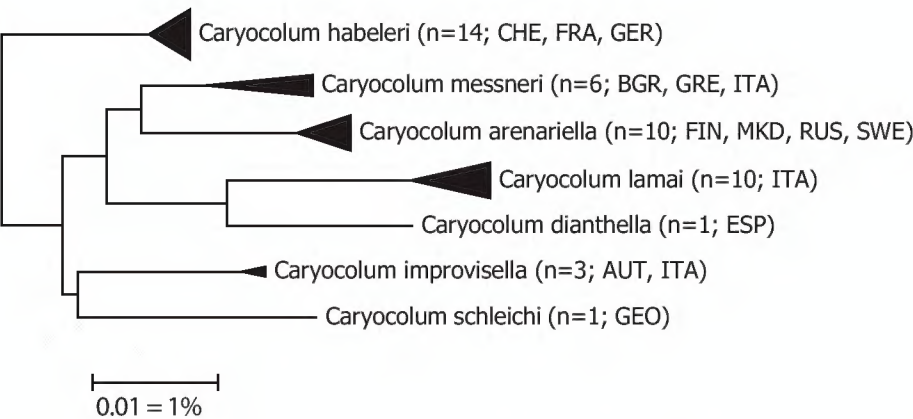


Figure 2. Neighbor-Joining tree of species in the *Caryocolum schleichi* species group (Kimura 2 parameter, built with MEGA 6 cf. Tamura et al. 2013), only sequences (>500 bp) considered. Note: the scale bar only applies to internal branches between species. Width of triangles represent sample size, depth the genetic variation within the cluster. Source: DNA Barcode data from BOLD (Barcode of Life Database, cf. Ratnasingham and Hebert 2007).

***Caryocolum schleichi* (Christoph, 1872)**

Lita schleichi Christoph 1872: 22, pl. 1, fig. 19. Lectotype ♂, Russia (NHM) [examined]. Designated by Huemer (1988).
Caryocolum syriacum Povolný 1977: 171, figs 1, 2, 6. Holotype ♂, Syria (MMB) [examined]. Synonymized by Huemer (1988).

Material examined. Lectotype ♂ (*schleichi*), Russia: Krasnoarmeysk, [40 km S. of Volgograd] (‘S-Russia, Sarepta’), 22 Jul.1868 (Christoph) (NHM).
Holotype ♂ (*syriacum*), Syria: Damascus, airport area, 28 May 1965, leg. Povolný (MMB).
Georgia: 1 ♂, Tbilisi, slopes S of, 600 m, 26 Aug. 1989, leg. Karisch, DNA Barcode TLMF Lep 22505 (TLMF).

Iran: 1 ♂, 28 km N Sanandaj, 1600 m, 15 Jun. 1975 leg. Amsel (TLMF). Jordan: 1 ♀, Amman, 890 m, 17 May 1958, leg. Klapperich (TLMF). Russia: 3 ♂♂ (*schleichi* paralectotypes), Krasnoarmeysk [40 km S. of Volgograd], 24 Jul. 1859, 31 Jul 1864, 1865, leg. Christoph; 4 ♂♂, 2 ♀♀, same locality, 16 Jun. 1873, 5 Sep. 1874, leg. Christoph (NHM). Syria: 1 ♂, 1 ♀, 25 km W. of Damaskus, 2–3 Jun. 1961, 8 Jun. 1961, leg. Kasy & Vartian (TLMF). Turkey: 1 ♂, Prov. Sivas, Gürün, 28 Jun. 1976, leg. Pinker (ZSM); 1 ♂, Prov. Sivas, 10 km W Gürün, 1650 m, 27 Jul. 1989, leg. Fibiger & Esser; 1 ♂, Prov. Sivas, Darende, Gününar, 900 m, 18 Oct. 1986, leg. Moberg & Hillmann; 1 ♀, Prov.Konya, 20 km SE Hadim, 1800 m, 14 Jul. 1986, leg. Fibiger (all ZMUC).

Diagnosis. *C. schleichi* can be easily separated from other species of the group by the white head, thorax and tegulae (but see below for material from Turkey). The male genitalia are particularly characterized by the massive valva, with a short and broadly pointed dorso-apical process. In this character the species is most similar to *C. habeleri* with a more slender, spine-like dorso-apical process of the valva and to *C. dianthella* with a smaller and dorsally concave valva with shorter and more slender dorso-apical and ventro-apical processes. Further, the sacculus of *C. schleichi* is shorter and stouter than in *C. dianthella* and *C. habeleri*. In all other species of the *C. schleichi* species group, the valva is more slender with a much longer dorso-apical process and a more slender dorso-ventral process. The female genitalia are almost indistinguishable from other species of the *C. schleichi* species group, except for the apophysis anterior which distinctly exceeds the length of segment VIII by about one-quarter, whereas it is of about the same length in all other species

Table 1. Intraspecific mean K2P (Kimura 2 Parameter) divergences, maximum pairwise distances, nearest species, nearest neighbor and distance to nearest neighbor.

Species	Mean Intra-Sp	Max Intra-Sp	Nearest Species	Nearest Neighbor	Distance to NN %
<i>Caryocolum arenariella</i>	0.58	1.25	<i>Caryocolum messneri</i>	LEASU048-18	2.35
<i>Caryocolum dianthella</i>	N/A	0	<i>Caryocolum messneri</i>	LECRT124-16	3.25
<i>Caryocolum habeleri</i>	0.52	1.1	<i>Caryocolum improvisella</i>	LEAST641-17	3.33
<i>Caryocolum improvisella</i>	0.31	0.46	<i>Caryocolum messneri</i>	LECRT124-16	3.15
<i>Caryocolum lamai</i>	0.62	1.44	<i>Caryocolum dianthella</i>	PHLSA085-11	3.43
<i>Caryocolum messneri</i>	0.87	1.71	<i>Caryocolum arenariella</i>	LEFIJ779-10	2.35
<i>Caryocolum schleichi</i>	0.77	0.77	<i>Caryocolum improvisella</i>	LEATF082-14	3.3

except for *C. dianthella* from which it differs by the narrower signum-hook.

Description. Adult (Fig. 3). Forewing length ♂ 4.5–6.5 mm, ♀ 4.5–5.0 mm. Head cream-white; labial palpus predominantly cream-white, dark brown mottling on outer surface of segment one, light brown mottling on outer surface of segment two and dark brown mixed with cream on segment three; antenna black, weakly ringed paler. Thorax and tegula white, occasionally mottled with light brown, few dark brown scales anteriorly. Abdomen cream-white on ventral surface. Forewing dark brown, mottled with greyish white on dorsal margin; cream-white transverse fascia from fold to costa at one-fifth; cream-white medial area frequently extended towards costa and dorsal margin; cream-white costal and tornal spots usually separate; fringes basally dark brown, distal part lighter. Hindwing light grey.

Variation. Specimens from Turkey frequently exhibit a darker head and thorax (Huemer and Karsholt 2010) and the taxonomic status of such specimens should be re-evaluated in future from more extensive material and molecular data.

Male genitalia (Figs 13, 21). Uncus broadly sub-quad-rangular, posterior corners rounded; lateral sclerites of gnathos distinct, medial part with large minutely spined culcitula; tegumen weakly widened anteriorly, with concavely emarginated anterior margin; transtilla sclerotized, longitudinally folded; pedunculus large, ear-shaped, with sclerotized inner edge; valva nearly straight, moderately long, massive, distal part broadly shovel-shaped, apex with two processes, short and broadly pointed dorsal and broadly digitate ventral process, medially separated by concave excavation; sacculus short, knife-shaped; posterior margin of vinculum deeply incised medially, with pair of long digitate processes, pair of latero-medial processes broadly projected; saccus slightly longer than valva, slender, gradually tapered to apex; phallus long, slender, nearly straight, apically with area of small cornuti.

Female genitalia (Figs 29, 36, 43). Apophysis posterior about three times length of apophysis anterior; segment VIII without processes, smooth; ostium bursae with short lateral folds; apophysis anterior 1.2 times length of segment VIII; antrum short, about one-fifth length of apophysis anterior, funnel-shaped; posterior part of ductus bursae with pair of long lateral sclerites extending to about apex of apophysis anterior, membranous part of ductus bursae about length of segment VIII including apophysis anterior; signum on right side of entrance to sub-oval corpus bursae, with broad base and moderately short, strongly bent hook.

Molecular data. BIN: [BOLD:ADH6455](#). The intra-specific average distance of the barcode region is 0.8%, the maximum distance 0.8% (p-dist) (n = 2). The minimum distance to the nearest neighbor, *C. arenariella*, is 3.37%.

Distribution (Fig. 1). Confirmed records are known from south-western Russia to Turkey and parts of Syria. A record from Macedonia (Klimesch 1968) probably refers to *C. arenariella*. The taxonomy of some populations

from the Near and Middle East requires further revisionary work. Huemer (1988) had already suspected an additional subspecies from northern Syria and Afghanistan but due to the lack of material and in absence of molecular data this problem has to be re-assessed in the future.

Bionomics. Host-plant and early stages are unknown, but it is suspected that the larva feeds on *Dianthus* similar to other species of the *C. schleichi* species group. *C. schleichi* is most probably restricted to warm and sunny habitats at low elevations to about 1800 m, but precisely documented observations to the habitat are missing. Moths have been collected from late May to October.

Remarks. *Lita schleichi* was described from an unspecified number of specimens from south-western Russia (Christoph 1872) with the lectotype selected by Huemer (1988). *Caryocolum syriacum* was described from Syria and the holotype fixed in the original description (Povolný 1977).

Caryocolum dianthella (Chrétien, 1925) stat. rev.

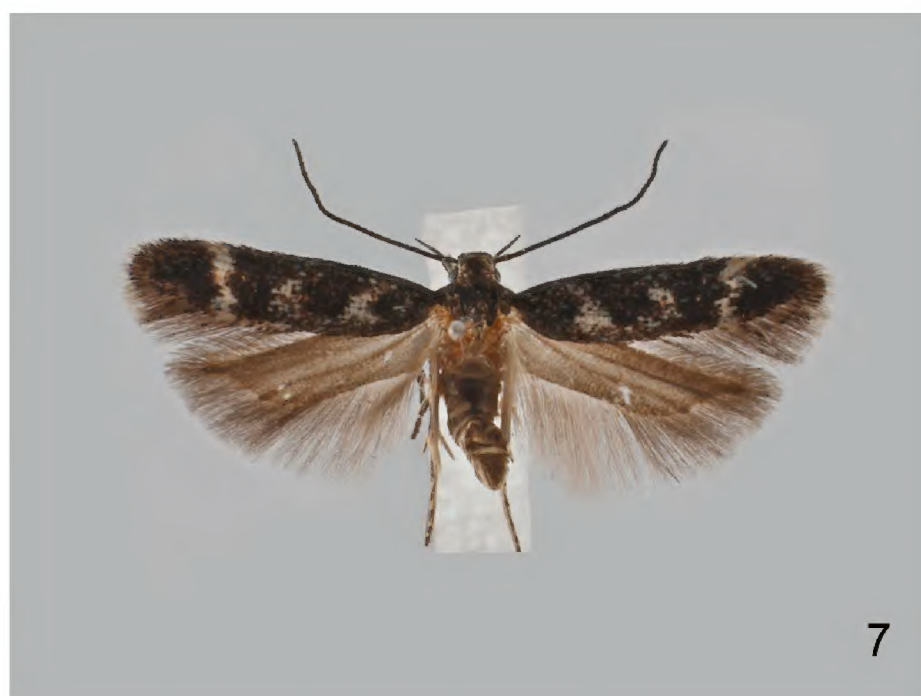
Lita dianthella Chrétien 1925: 246. Syntypes, Spain: Segovia, La Granja de San Ildefonso (MNHN) [not examined].

Caryocolum hackeri Derra 1985: 373, figs 1, 4–6. Holotype ♂, Spain (coll. Derra, Bamberg). Synonymized by Huemer 1988: 489.

Material examined. Holotype ♂ (*hackeri*), Spain: Pyrenees, Lerida province, Bellver de Cerdanya, 900 m, 20 Sep. 1981, leg. Derra, genitalia slide no. 86/248 P. Huemer (coll. Derra, Bamberg).

Andorra: 1 ♀, La Massana, 2 Jun. 2002 e.l. (*Dianthus pungens*), leg. Mazel (TLMF). Spain: 1 ♂, 1 ♀ (paratypes *hackeri*), same data as holotype but 7 Oct 1981, leg. Derra (coll. Derra, Bamberg); 1 ♀, Zaragoza province, 3 km E Cerveruela, Rio del Huerva, 800 m, 6 Sep. 2001, leg. Skule & Skou (TLMF); 1 ♂, Alicante province, Alcoj, Font Roja, W El Menejador, S slope, 1300 m, 4 Sep. 2005, leg. Huemer (TLMF); 2 ♂♂, 6 ♀♀, Granada province, Camino de Capileira, 1250 m, 13 Jul. 1985, leg. Baldizzone & Traugott-Olsen; 2 ♂♂, Granada province, Sierra Nevada, Puerto de la Ragua, 1000 m, 25 Jun. 1968, 20 Jul. 1969, leg. Sattler & Carter; 2 ♂♂, 1 ♀, Granada province, Sierra de Alfacar, 1500 m, 3 Jul. 1962, 13 Sep. 1972, leg. Sattler; 1 ♂, Huesca province, Jaca, 12 Aug. 1933, leg. Fassnidge (all NHM); 5 ♂♂, 1 ♀, Granada province, Sierra Nevada, Cam. de Veleta, 2000–2300 m, 24 Jul. 1983, 19 Aug. 1984, leg. Traugott-Olsen (ZMUC, TLMF); 1 ♂, 1 ♀, Granada province, Sierra Nevada, Cam. de Veleta, 2250–2300 m, 1 Aug. 1986, leg. Traugott-Olsen; 1 ♂, Granada province, Sierra Nevada, Ruta del Veleta, 1600 m, 19 Sep. 1987 (all TLMF). France: 2 ♂♂, 1 ♀, Pyrénées-Orientales, Thuès-les-Bains, larvae 24 Jun. 1900 on *Dianthus*, moths emerged 26 Jul. 1900, leg. Walsingham (NHM). Morocco: 1 ♂, Haut Atlas, Oukaïmeden, 2600 m, 9 & 11 Jul. 1975, leg. Kasy (NHMW).

Diagnosis. *C. dianthella* differs from *C. schleichi* by the brown rather than white head, thorax and tegulae but



Figures 3–8. Adults. **3** *Caryocolum schleichi*, male, Syria; **4** *C. dianthella*, male, Spain; **5** *C. improvisella*, male, Austria; **6** *C. improvisella*, female, Austria; **7** *C. arenariella*, male, Sweden; **8** *C. arenariella*, female, Sweden.

cannot be reliably separated from the other species of the complex by external characters. However, the male genitalia are characterized by the shape of the valva, particularly the convex dorsal margin with a sub-apical hump, the shortly pointed sub-dorsal process and the small digitate ventral process. A similarly short but broader dorso-apical process is only found in *C. schleichi*, whereas *C. habeleri* with a similar dorso-apical process differs in the large ventro-apical projection and the weakly curved

dorsal margin of the valva. In all other species of the *C. schleichi* species group, the valva is more slender with a much longer dorso-apical process and a more slender dorso-ventral process. The female genitalia are almost indistinguishable from other species of the *C. schleichi* species group except for the characteristic signum with a broad hook and a largely reduced base.

Description. Adult (Fig. 4). Forewing length ♂ 4.0–5.5 mm, ♀ 4.0–5.0 mm. Head dark brown, frons cream-

white to white; labial palpus dark brown, second segment cream-white on inner and upper surface, mottled with grey-brown on outer surface, third segment dark brown mottled with few white scales; antenna black, weakly ringed paler. Thorax and tegula rusty brown, anterior part dark brown. Abdomen predominantly grey on ventral surface, medially cream-coloured. Forewing dark brown with weak light mottling, distinct white markings: transverse fascia from fold to costa at one-fifth, distinct white medial spot, separate costal and tornal spots; fringes basally dark brown, distal part lighter. Hindwing light grey.

Variation. Weak variation in the extent of the white markings.

Male genitalia (Figs 14, 22). Uncus broadly sub-quad-rangular, posterior corners rounded; lateral sclerites of gnathos distinct, medial part with large minutely spined culcitula; tegumen weakly widened anteriorly, with slightly emarginated anterior margin; transtilla sclerotized, longitudinally folded; pedunculus large, sub-triangular, with sclerotized inner edge; valva nearly straight, moderately long, distal part moderately broad, shovel-shaped, dorsal edge with distinct convex hump, apex with two processes, short pointed sub-dorsal and small digitate ventral process, medially separated by small excavation; sacculus moderately long, knife-shaped; posterior margin of vinculum deeply incised medially, with pair of long digitate processes, pair of latero-medial processes broadly projected; saccus slightly longer than valva, slender, gradually tapered to apex; phallus long, slender, nearly straight, apically with area of small cornuti.

Female genitalia (Figs 30, 37, 44). Apophysis posterior about four times length of apophysis anterior; segment VIII without processes, smooth; ostium bursae with short lateral folds; apophysis anterior 1.3 times length of segment VIII; antrum short, about one-fifth length of apophysis anterior, funnel-shaped; posterior part of ductus bursae with pair of long lateral sclerites extending to about apex of apophysis anterior, membranous part of ductus bursae about length of segment VIII including apophysis anterior; signum on right side of entrance to sub-oval corpus bursae, with broad base lacking crescent-shaped lateral projections, and stout hook.

Molecular data. BIN: [BOLD:AAU1854](#). The intra-specific average distance of the barcode region is 1.43%, the maximum distance 1.83% (p-dist) (n = 3). The minimum distance to the nearest neighbor, *C. lamai*, is 3.05%.

Distribution (Fig. 1). *C. dianthella* is restricted to the Western Mediterranean, with country records from Morocco, Portugal, Spain and France (Pyrenees).

Bionomics. The larva has been recorded in May and June feeding on *Dianthus scaber toletanus* (Boiss and Reuter) Tutin and *D. deltoides* L. and moths emerged in July (Chrétien 1925). In the Pyrenees it was also bred from *Dianthus pungens* L. (see material examined). In the field moths have been collected from late June to October up to altitudes of about 2600 m in Morocco.

Remarks. *Lita dianthella* was described from an unspecified number of specimens from central Spain (Chrétien 1925) and the genitalia of a syntype figured by Agenjo (1962) leave no doubt as to the identity. *Caryocolum hackeri* was described from northern Spain (Pyrenees) with the holotype fixed in the original description (Derra 1985).

***Caryocolum improvisella* (Rebel, 1936) stat. rev.**

Lita improvisella Rebel 1936: 3, pl. 1, fig. 7. Lectotype ♂, Switzerland: Graubünden, Remüs (Unterengadin), 21.vii.1931, leg. Thomann (BNCH) [here designated, not traced].

Material examined. Austria: 1 ♂, 3 ♀, Tirol, Zams, Steinseehüttenweg, 1000 m, 17 Sep. 1987, leg. Huemer; 1 ♂, Tirol, Vennatal, 1500 m, e.l. 2.viii.1956 (*Dianthus sylvestris*), leg. Burmann; 1 ♂, 4 ♀, same data, but 850 m, 13 Aug. 1988, leg. Burmann & Huemer; 1 ♂, same data, but 47°10'35"N, 10°36'14"E, 29 Jul. 1989, leg. Burmann; 1 ♂, Tirol, Fließ, Vögele Bichl, 47°6'57"N, 10°37'35"E, 23 Jul. 2014, DNA Barcode TLMF Lep 15322, gen. slide GEL 1256 ♂ P. Huemer; 2 ♂, Tirol, Umhausen, unterh. Farst, 1100 m, 47°9'25"N, 10°55'22"E, 5 Sep. 2013, DNA Barcode TLMF 13394, gen. slide in glycerin; 1 ♀, Tirol, Umhausen, 1500 m, 9 Jul. 1948 e.l. (*Dianthus sylvestris*), leg. Burmann, gen. slide GU 86–109 ♀ P. Huemer; 1 ♀, same data, but 10 Jul. 1948 e.l., gen. slide GU 86–109 ♀ P. Huemer; 1 ♀, same data, but 15 Jul. 1948 e.l.; 1 ♀, same data, but 19 Jul. 1948 e.l. Italy: 3 ♂, Südtirol province, Laas, 5 Jul. 1987 e.l. (*Dianthus*) leg. Huemer, gen. slide GEL 1290 ♂ P. Huemer; 1 ♂, same data, but 2 Jul. 1987 e.l. (*Dianthus*); 1 ♀, same data, but 14 Jul. 1987 e.l. (*Dianthus*); 1 ♀, Südtirol province, Laatsch, 1000 m, 19 Aug. 1972, leg. Burmann; 1 ♀, Südtirol province, Matschertal, Waalweg, 1750 m, 46°42'44"N, 10°38'32"E, 24 Aug. 2017, leg. Huemer, DNA Barcode TLMF Lep 23714 (all TLMF).

Diagnosis. *C. improvisella* differs from *C. schleichi* by the brown rather than white head, thorax and tegulae. It is usually larger than *C. arenariella* and *C. lamai* but otherwise cannot be reliably separated from the other species of the complex by external characters. The male genitalia are characterized in particular by the distally widened valva with a moderately long, pointed dorsal process, a character which is only shared with *C. arenariella*, *C. messneri*, and *C. lamai*. However, this process is distinctly shorter than in *C. arenariella* and *C. lamai*. The species differs from *C. messneri* in several characters such as the broader valva with a longer dorsal process and the distinctly shorter latero-medial processes of the vinculum. The female genitalia are hardly discernible from several other species of the *C. schleichi* species group though the short crescent shaped base of the signum in combination with the moderately slender signum hook seem characteristic and differ from all other species except for *C. messneri*. However, the individual variation of these characters is insufficiently documented due to lack of material.

Description. Adult (Figs 5, 6). Forewing length ♂ 5.5–7.0 mm, ♀ 4.5–6.0 mm. Head with dark grey-brown vertex, mottled with white, frons cream-white; first seg-



Figures 9–12. Adults. **9** *Caryocolum lamai*, paratype, male, Italy; **10** *C. lamai*, paratype, male, Italy; **11** *C. messneri*, paratype, male, Italy; **12** *C. habeleri*, paratype, male, France.

ment of labial palpus dark brown, second segment cream-white on inner and upper surface, ventral and outer surface predominantly dark brown, dark brown mixed with few whitish scales on segment three; antenna black, weakly ringed paler. Thorax and tegula dark brown anteriorly, posterior half mixed cream with dark brown and some rusty brown mottling. Abdomen grey to whitish grey on ventral surface. Forewing dark brown, mottled with greyish white on dorsal margin; white transverse fascia from fold to costa at one-fifth; white medial spot occasionally extended towards costal and dorsal margin; white costal and tornal spots separate; fringes basally dark brown, distal part paler. Hindwing light grey.

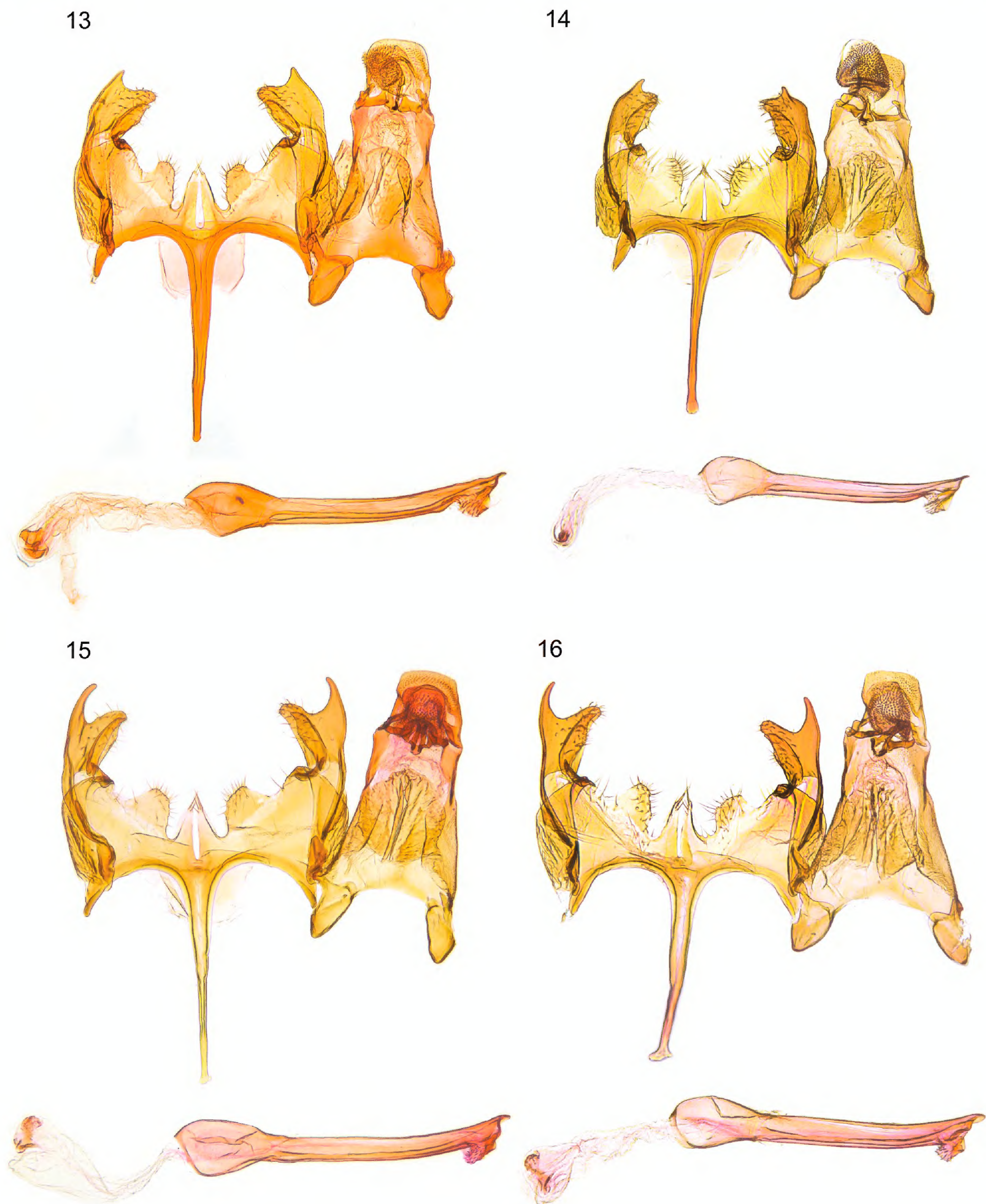
Variation. The extension of white markings of the forewings varies considerably.

Male genitalia (Figs 15, 16, 23, 24). Uncus broadly sub-quadrangular, posterior corners rounded; lateral sclerites of gnathos distinct, medial part with large minutely spined culcitula; tegumen weakly widened anteriorly, with slightly emarginated anterior margin; transtilla sclerotized, longitudinally folded; pedunculus large, sub-oval, with sclerotized inner edge; valva nearly straight, long, distal part broadly dilated with weakly curved dorsal and straight ventral edges, apex with two processes,

moderately long and pointed dorsal process extended to about middle of uncus, broadly digitate ventral process at about right-angles to and about length of dorsal process; saccus moderately long, slender, with parallel margins, apically pointed; posterior margin of vinculum deeply incised medially, with pair of moderately long digitate processes, pair of latero-medial processes broadly hump-like; saccus slightly longer than valva, slender, gradually tapered to apex; phallus long, slender, nearly straight, apically with area of small cornuti.

Female genitalia (Figs 31, 38, 45). Apophysis posterior about four times length of apophysis anterior; segment VIII without processes, smooth; ostium bursae with short lateral folds; apophysis anterior about length of segment VIII; antrum short, about one-fifth length of apophysis anterior, funnel-shaped; posterior part of ductus bursae with pair of long lateral sclerites extending to about apex of apophysis anterior, membranous part of ductus bursae about length of segment VIII including apophysis anterior; signum on right side of entrance to sub-oval corpus bursae, with broad and shortly crescent-shaped base and moderately slender hook.

Molecular data. BIN: [BOLD:ACL3018](#). The intraspecific average distance of the barcode region is



Figures 13–16. Male genitalia. **13** *Caryocolum schleichi*, Syria, slide GU 86/273 P. Huemer; **14** *C. dianthella*, Spain, slide GEL 1284 P. Huemer; **15** *C. improvisella*, Austria, slide GEL 1256 P. Huemer; **16** *C. improvisella*, Italy, slide GEL 1290 P. Huemer.

0.31%, the maximum distance 0.46% (p-dist) ($n = 3$). The minimum distance to the nearest neighbor, *C. messneri*, is 3.05%.

Distribution (Fig. 1). The species is currently only known from a small section of the Central Alps of Switzerland, Italy and Austria.

Bionomics. The larva has been recorded feeding within shoots of *Dianthus sylvestris* Wulfen (Klimesch 1953; Burmann 1990; pers. obs.) and moths emerged from early July to the beginning of August. The species has been recorded along steep rock-surface on siliceous soil in the montane zone.

17



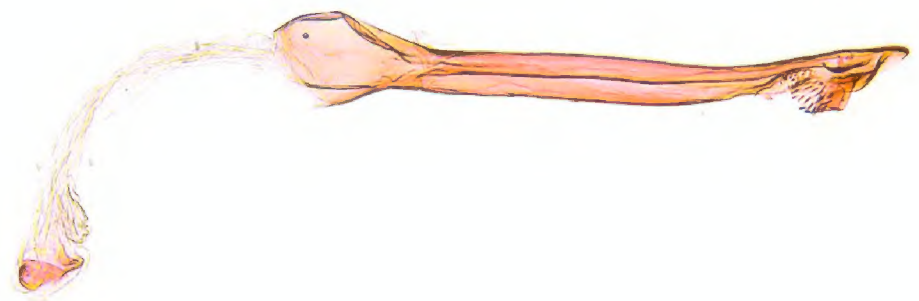
18



19



20



Figures 17–20. Male genitalia. **17** *Caryocolum arenariella*, Russia, slide GEL 1260 P. Huemer; **18** *C. messneri*, holotype, Italy, slide GEL 1255; **19** *C. lamai*, paratype, Italy, slide GEL 1258 P. Huemer; **21** *C. habeleri*, paratype, France, slide GEL 1289 P. Huemer.

Remarks. *Lita improvisella* was described from 1 ♂ and 1 ♀ collected at two different localities in Switzerland (Graubünden) by Thomann, and a further in-

correctly identified specimen probably of *C. leucomelanella* from Valais, with the genitalia figured in the original description (Rebel 1936). Klimesch (1953)

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Figures 21–24. Male genitalia (details vinculum-valva-complex). **21** *Caryocolum schleichi*, Syria, slide GU 86/273 P. Huemer; **22** *C. dianthella*, Spain, slide GEL 1284 P. Huemer; **23** *C. improvisella*, Austria, slide GEL 1256 P. Huemer; **24** *C. improvisella*, Italy, slide GEL 120 P. Huemer.

figured the male genitalia of a syntype from Remüs, which is here designated as the lectotype in order to fix the identity. The second specimen from Landquart,

1.vii.1922, leg. Thomann, probably belongs to *C. habeleri*, a species which has been collected nearby in the Swiss Rhine valley.

***Caryocolum arenariella* (Benander, 1937)**

Lita arenariella Benander 1937: 31, figs A, B. Syntypes, Sweden: Scania: Saltvik; Kivik; Borgeby, moths bred end of vii.1922 (larvae in *Dianthus arenarius* stems), leg. Benander [not traced].

Material examined. Sweden: 3 ♂♂, 2 ♀♀, Sk., Tyngsjö, 4 Sep. 1957, 24 Jul. 1965, leg. Svensson (ZCLU; NHM); 1 ♂, Sk., Vitemölla, 22–31 Jul. 1965, leg. Svensson (ZMUC); 1 ♂, same data, but 8 Jul. 1988 e.l. (*Dianthus arenarius*); 3 ♂♂, same data, but 11 Jul. 1988 e.l.; 2 ♂♂, 1 ♀, same data, but 12 Aug. 1988 e.l., gen. slide GEL 1292 ♀ P. Huemer; 1 ♂, same data, but 17 Jul. 1988 e.l. (all TLMF); 1 ♂, [Schonen,] Kivik, 20 Jun. 1964, leg. Benander (ZMUC). Latvia: 1 ♂, Mangalsala, 9 Aug. 1977, leg. Sulcs (ZMUC). North Macedonia: 2 ♂♂, NP Mavrovo, Korab, Korabska jezero, Kobilino pole, 2080–2180 m, 41°46'42"N, 20°34'55"E, 28 Jul. – 1 Aug. 2011, leg. Huemer & Tarmann, DNA Barcode TLMF Lep 05274 (TLMF). Russia: 13 ♂♂, Altai Republic, Kosh-Agach distr., 17 km NNE Kokorya vill., Talduair Mt., valley of Sajlyugem river, 2200 m, 50°01'N, 89°14'E, 30 Jul. – 2 Aug. 2016, leg. Huemer & Wiesmair, DNA Barcodes TLMF Lep 20329, 20330, 20331, gen. slides GEL 1259 ♂ P. Huemer, GEL 1260 ♂ P. Huemer; 1 ♂, Altai Republic, Kosh-Agach distr., Northern part of Ukok plateau, 2400–2500 m, 49°30'N, 88°05'E, 4–6 Aug. 2016, leg. Huemer & Wiesmair; 11 ♂♂, 1 ♀, Altai Republic, Ulagan distr., 10 km NE Aktash vill., Kuraj Mts. Range, 2150 m, 50°19'N, 87°43'E, 6–8 Aug. 2016, leg. Huemer & Wiesmair; 8 ♂♂, Altai Republic, Ulagan distr., 11 km NNW Aktash vill., Ajgulak Mts. Range, 1900 m, 50°25'N, 87° 34'E, 28–30 Jul. 2016, leg. Huemer & Wiesmair; 1 ♂, Burytia, Barguzin valley, Djirga st., 600 m, 54°55'N, 111°14'E, 10 Jul. 1996, leg. Jalava & Kullberg (all TLMF).

Diagnosis. *C. arenariella* is, besides *C. lamai*, the smallest and darkest species of the *C. schleichi* species group, with the white markings and brown scales reduced in many specimens. It differs from *C. schleichi* by the brown rather than cream-white head, thorax and tegulae but cannot be reliably separated from the other species of the complex by external characters. However, the male genitalia are characterized by the shape of the valva, particularly the long, pointed dorsal process, only shared with *C. improvisella*, *C. messneri*, and *C. lamai*. This process is more slender and longer than in *C. improvisella* and *C. messneri* whereas the male genitalia differ from *C. lamai* by the broader sacculus and the more slender and longer digitate medial processes of the vinculum. The female genitalia are hardly discernible from other species of the *C. schleichi* species group, except for the signum with a slender and long crescent-shaped base, a character only shared with *C. lamai*, and the particularly short apophysis posterior. However, the individual variation of this character is insufficiently documented due to lack of material.

Description. Adult (Figs 7, 8). Forewing length ♂ 4.0–5.0 mm, ♀ 3.5–4.5 mm. Head dark grey-brown, mottled with light grey, frons greyish white; labial palpus

dark brown, second segment cream-white on inner surface, third segment blackish, mottled with white; antenna black, weakly ringed paler. Thorax and tegula dark grey-brown. Abdomen dark grey on ventral surface. Forewing dark brown with some light mottling, particularly on dorsum; distinct white markings: narrow transverse fascia from fold to costa at one-fifth, irregular white medial spot, separate costal and tornal spots; fringes basally dark brown, distal part lighter. Hindwing light grey.

Variation. Specimens from Macedonia are larger (6.0 mm) and together with parts of Russian material exhibit some light mottling on the thorax and extended cream-white mottling of the forewing, particularly the dorsal area.

Male genitalia (Figs 17, 25). Uncus broadly sub-quadrangular, posterior corners rounded; lateral sclerites of gnathos distinct, medial part with large minutely spined culcitula; tegumen weakly widened anteriorly, with slightly emarginated anterior margin; transtilla sclerotized, longitudinally folded; pedunculus large, sub-triangular, with sclerotized inner edge; valva nearly straight, long, distal part moderately slender, weakly dilated with straight dorsal and ventral edges, apex with two processes, long and pointed dorsal process extended to posterior third of uncus, broadly digitate ventral process at about right-angles to dorsal process; sacculus moderately long, slender, with parallel margins, apically pointed; posterior margin of vinculum deeply incised medially, with pair of moderately short digitate processes, pair of latero-medial processes broadly projected; saccus slightly longer than valva, slender, gradually tapered to apex; phallus long, slender, nearly straight, apically with area of small cornuti.

Female genitalia (Figs 32, 39, 46). Apophysis posterior about 3.5 times length of apophysis anterior; segment VIII without processes, smooth; ostium bursae with short lateral folds; apophysis anterior about length of segment VIII; antrum short, about one-fifth length of apophysis anterior, funnel-shaped; posterior part of ductus bursae with pair of long lateral sclerites extending to about apex of apophysis anterior, membranous part of ductus bursae about length of segment VIII including apophysis anterior; signum on right side of entrance to sub-oval corpus bursae, with slender and long crescent-shaped base and long slender hook.

Molecular data. BIN: [BOLD:AAE9479](#). The intraspecific average distance of the barcode region is 0.6%, the maximum distance 1.31% (p-dist) (n = 10). The minimum distance to the nearest neighbor, *C. messneri*, is 2.25%.

Distribution (Fig. 1). Only known from scattered localities in Sweden, Finland, the Baltic countries (Aarvik et al. 2017), North Macedonia, and from southern Siberia.

Bionomics. The larva has been recorded in May, feeding in the stem of *Dianthus arenarius* L. which becomes gall-like stout and swollen (Benander 1926). Pupation takes place outside the gall on the ground surface. However, according to Mutanen (in litt.) larvae live within the stems, without causing a conspicuous swollen gall. In the field moths have been collected from late June to early September at artificial light sources.

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Figures 25–28. Male genitalia (details vinculum-valva-complex). **25** *Caryocolum arenariella*, Russia, slide GEL 1260 P. Huemer; **26** *C. messneri*, holotype, Italy, slide GEL 1255; **27** *C. lamai*, paratype, Italy, slide GEL 1258 P. Huemer; **28** *C. habeleri*, paratype, France, slide GEL 1289 P. Huemer.

Remarks. *Lita arenariella* was described from an unspecified number of specimens and no syntypes have been traced. However, the detailed description of the moth, genitalia and biology (Benander 1926) leave no doubt about the identity of this species. The taxon was re-instated at species level by Aarvik et al. (2017).

***Caryocolum messneri* sp. nov.**

<http://zoobank.org/BEDFE053-00A6-4904-8F94-E0EF8AF4E716>

Material examined. Holotype ♂, “ITALIA sept. Südtirol / Schnals, Neu-Ratteis, / Fuchsberg, 980 m / 10°56'42"E, 46°40'27"N / 650 m, 28.8.2014 / leg. Huemer” “DNA Barcode / TLMF Lep 16694” “P. Huemer / GEL 1255 ♂” (TLMF).

Paratypes: Italy: 1 ♂, same data as holotype, but DNA Barcode TLMF Lep 16694; 1 ♂, 3 ♀♀, Südtirol province, Schnalstal, unt. Ladurner, 650 m, 31 Aug. 2019, leg. Huemer, DNA Barcodes TLMF Lep 23981, 23982, 4 gen. slides in glycerin; 1 ♂, Trento province, Villamontagna, 600 m, 17 Aug. 1982, leg. Burmann, gen. slide GU 86/035 ♂ P. Huemer (all TLMF). Bulgaria: 1 ♀, Triglav env., 1240 m, 4 Aug. 2013, leg. Karsholt & Zlatkov, DNA Barcode TLMF Lep 21297 (ZMUC). Greece: 1 ♀, Epirus, Mitsikeli Mt. near Joannina, 1400 m, 39°46'15"N, 20°48'20"E, 8 Jul. 2005, leg. Mayr (RCTM).

Diagnosis. *C. messneri* differs from *C. schleichi* by the brown rather than cream-white head, thorax and tegulae. It is usually larger than *C. arenariella* and *C. lamai* and the medial spot is less sharply delimited than in *C. dianthella*. Otherwise, *C. messneri* cannot be reliably separated from the other species of the complex by external characters, though the usually well developed rusty-brown mottling seems unique. The male genitalia are characterized in particular by the moderately long, pointed dorsal process of the valva, a character which is only shared with *C. improvisella*, *C. arenariella*, and *C. lamai*. However, this process is distinctly shorter than in *C. arenariella* and *C. lamai*. The species further differs from *C. improvisella* in several characters such as the more slender valva with parallel outer edges and a distodorsal bulge, a shorter dorsal process, and the distinctly longer latero-medial processes of the vinculum. The female genitalia are hardly discernible from several other species of the *C. schleichi* species group though the shortly crescent-shaped base of the signum in combination with the moderately slender signum hook seem characteristic and differ from all other species except for *C. improvisella*. However, the individual variation of these characters is insufficiently documented due to lack of material.

Description. Adult (Fig. 11). Forewing length ♂ 5.5–6.0 mm, ♀ 5.0 mm. Head with dark grey-brown vertex, mottled with white, frons cream-white; first segment of labial palpus dark brown, second segment cream-white on inner and upper surface, ventral and outer surface predominantly dark brown, dark brown mixed with few whitish scales on segment three; antenna black, weakly ringed paler. Thorax and tegula dark brown anteriorly, posterior half cream with rusty brown mottling. Abdomen

cream-white with some grey on ventral surface. Forewing dark brown, mottled with white on dorsal margin; basal two thirds with rusty-brown mottling, particularly white markings; white transverse fascia from fold to costa at one-fifth; white medial spot occasionally extended towards costa and dorsal margin; white costal and tornal spots separate; fringes basally dark brown, distal part paler. Hindwing light grey.

Variation. In the limited available material, the extent of rusty-brown mottling shows some variation.

Male genitalia (Figs 18, 26). Uncus broadly sub-quadangular, posterior corners rounded; lateral sclerites of gnathos distinct, medial part with large minutely spined culcitula; tegumen weakly widened anteriorly, with slightly emarginated anterior margin; transtilla sclerotized, longitudinally folded; pedunculus large, sub-triangular, with sclerotized inner edge; valva nearly straight, long, moderately slender distal part with parallel edges, except for bulged disto-dorsal edge, apex with two processes, stout and moderately long and pointed dorsal process extended to about middle of uncus, broadly digitate ventral process at about right-angles to and slightly longer than dorsal process; sacculus moderately long, slender, with parallel margins, apically pointed; posterior margin of vinculum deeply incised medially, with pair of moderately long digitate processes, pair of latero-medial processes moderately broad, digitate, distinctly projected; saccus slightly longer than valva, slender, gradually tapered to apex; phallus long, slender, nearly straight, apically with area of small cornuti.

Female genitalia (Figs 33, 40, 47). Apophysis posterior almost five times length of apophysis anterior; segment VIII without processes, smooth; ostium bursae with short lateral folds; apophysis anterior about length of segment VIII; antrum short, about one-fifth length of apophysis anterior, funnel-shaped; posterior part of ductus bursae with pair of long lateral sclerites extending to about apex of apophysis anterior, membranous part of ductus bursae about length of segment VIII including apophysis anterior; signum on right side of entrance to sub-oval corpus bursae, with broad and shortly crescent-shaped base and moderately slender hook.

Molecular data. BIN: **BOLD:ACT3307**. The intraspecific average distance of the barcode region is 1.18%, the maximum distance 1.77% (p-dist) (n = 4). The minimum distance to the nearest neighbor, *C. arenariella*, is 2.25%.

Etymology. The species is named in honour of Reinhold Messner, the first climber to ascend all fourteen peaks above 8000 metres sea level and living in the neighborhood of the type locality of the new species.

Distribution (Fig. 1). The species is currently only known from a restricted area in northern Italy (region of Trentino-Alto Adige) and from specimens collected in Slovenia, Bulgaria and Greece.

Bionomics. Host-plant and early stages are undescribed but it seems most likely that the species shows a similar behaviour as related taxa with a hostplant restriction to *Dianthus* spp. At the type-locality *Dianthus sylvestris* Wulfen has been recorded. The adults have been



Figures 29, 30. Female genitalia. **29** *Caryocolum schleichii*, Syria, slide GU 86/277 P. Huemer; **30** *C. dianthella*, Spain, slide GEL 1285 P. Huemer.

found from mid to late August nearby rocks on siliceous soil where they were attracted to artificial light sources.

***Caryocolum lamai* sp. nov.**

<http://zoobank.org/CE0385B3-C608-48F3-9DEA-67824816B44E>

Material examined. Holotype ♂, “ITALIA sept., prov. Torino / PN del Gran Bosco di / Salbertrand, 2 km SE Colle / dell’ Assieta, 2240 m / 6°58'44"E, 45°3'38"N / 25.7.2019,

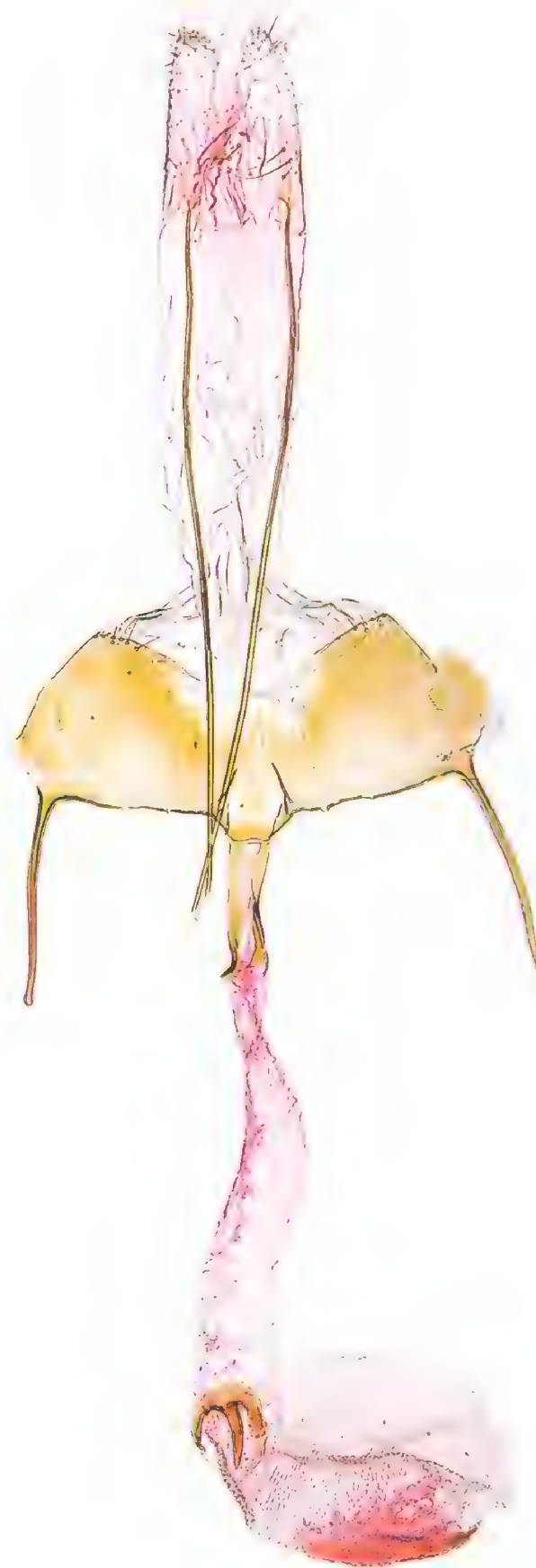
leg. Huemer / TLMF 2019-026” “DNA Barcode / TLMF Lep 27645” “P. Huemer / GEL 1283 ♂” (TLMF).

Paratypes: Italy: 7 ♂♂, same data as holotype, but DNA Barcodes 27646, 27647 (TLMF); 21 ♂♂, 1 ♀, Cuneo province, Val Traversagn, Casteldelfino W, 2050, 44°34'00"N, 6°58'30"E, 21 Jul. 2001, leg. Huemer, gen. slides GEL 1258 ♂, GEL 1262 ♂, GEL 1286 ♀ (TLMF); 12 ♂♂, same data, but leg. Mayr (RCTM); 1 ♂, same data, but S. Anna, 21–22 Jul. 2001, leg. Huemer (TLMF); 9 ♂♂, Cuneo province, Demonte NW, Colle Fauniera

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Figures 31, 32. Female genitalia. **31** *Caryocolum improvisella*, Italy, slide GEL 1291 P. Huemer; **32** *C. arenariella*, Sweden, slide GEL 1292 P. Huemer.

env., 2480–2500 m, 44°23'08"N, 7°7'19"E, 3 Aug. 2008, leg. Huemer, DNA Barcodes TLMF Lep 00107, 00108, 03747, 03748, 03749, 2 gen. slides in glycerin (TLMF);

2 ♂, same data, but 19 Jul. 2016, leg. Schmid, DNA Barcodes TLMF Lep 22437, 22438 (RCJS); 5 ♂♂, Cuneo province, Gias Valcavera, 2050 m, 44°22,6'N, 07°06,2'E,



Figures 33–35. Female genitalia. **33** *Caryocolum messneri*, paratype, Italy, slide GEL 1295 P. Huemer; **34** *C. lamai*, paratype, Italy, slide GEL 1286 P. Huemer; **35** *C. habeleri*, paratype, Germany, slide M 1703.

23 Jul. 2009, leg. Mayr; 32 ♂♂, same data, but 27 Jul. 2009; 1 ♂, same data, but 17 Aug. 2012; 3 ♂♂, same data, but 15 Aug. 2019 (all RCTM); 3 ♂♂, same data, but 23 Jul. 2009, leg. Huemer, DNA Barcode TLMF Lep 00533 (TLMF); 6 ♂♂, Cuneo province, Colle Valcavera, 2450 m, 44°22,9'N, 07°07,2'E, 28 Jul. 2015, leg. Mayr (RCTM); 1 ♂, same data, but 2400–2450 m, 5 Aug. 2008, leg. Huemer; 12 ♂♂, Colle Valcavera NE, 2450 m, 44°23'04"N,

07°06'23"E, 17 Aug. 2012, leg. Huemer (TLMF); 9 ♂♂, Cuneo prov., N Colle della Lombarda, 2370 m, 44°12.12'N, 7°08.64'E, 18–19 Aug. 2012, leg. Huemer, gen. slide in glycerin (TLMF); 9 ♂♂, Torino province, PN Orsiera – Rocciavrè, Usseaux, Colle delle Finestre N, 2180 m, 45°4'21"N, 7°3'11"E, 24 Jul. 2019, leg. Huemer (TLMF); 3 ♂♂, 1 ♀, Torino province, Via Colle delle Finestre, Pequerel NE, 1840 m, 45°3'7.65"N, 7°4'16.27"E, 26

Aug. 2019, leg. Wieser (LMK); 28 ♂♂, Torino province, Testa dell Assietta, 2530 m, 45°3'49.56"N, 6°57'2.79"E, 25 Aug. 2019, leg. Wieser (LMK); 1 ♂, Torino prov., Meana di Susa, Piano del Tiraculo, 2000 m, 25 Jul. 2007, leg. Baldizzone (TLMF). France: 22 ♂♂, Dep. Alpes-Maritimes, Col de la Lombarde, 2350 m, 44°12'8"N, 7°9'E, 18–19 Aug. 2012, leg. Huemer, gen. slide in glycerine; 2 ♂♂, Dep. Alpes-Maritimes, PN Mercantour, N Col de la Cayolle, Col de la Boucharde N, 1930–1950 m, 44°17'N, 6°44'36"E, 26 Jul. 2009, leg. Huemer; 1 ♂, Alpes-de-Haute-Provence, Col d'Allos, 2400 m, 21 Jul. 1999, leg. J. Nel, gen. slide 9458 ♂ J. Nel (all TLMF).

Diagnosis. *C. lamai* is, together with *C. arenariella*, the smallest and darkest species of the *C. schleichi* species group with reduced white markings and brown scales. It differs from *C. schleichi* by the brown rather than white head, thorax and tegulae but cannot be reliably separated from the other species of the complex by external characters of the forewings. However, the male genitalia are characterized by the shape of the valva, particularly the long, sharply pointed dorsal process, only shared with *C. improvisella*, *C. messneri* and *C. arenariella*. This process is more slender and longer than in *C. improvisella* and *C. messneri*, whereas the male genitalia differ from *C. arenariella* in particular in the more slender sacculus and the broader and the digitate medial processes of the vinculum. The female genitalia are hardly discernible from other species of the *C. schleichi* species group, except for the signum with a slender and long crescent-shaped base, a character only shared with *C. arenariella*, from which it differs by the longer apophysis posterior. However, the individual variation of this character is insufficiently documented due to lack of material.

Description. Adult (Figs 9, 10). Forewing length ♂ 4.5–5.5 mm, ♀ 4.0 mm. Head dark grey-brown, mottled with light grey, frons greyish white; labial palpus dark brown, second segment cream-white on inner surface, third segment blackish, mottled with white; antenna black, weakly ringed paler. Thorax and tegula dark grey-brown, with few rusty brown scales. Abdomen dark grey on ventral surface. Forewing dark brown with some light mottling, particularly on dorsum; distinct white markings: narrow transverse fascia from fold to costa at one-fifth, irregular white medial spot, separate costal and tornal spots; fringes basally dark brown, distal part lighter. Hindwing light grey.

Variation. The extension of light mottling of the forewing varies slightly.

Male genitalia (Figs 19, 27). Uncus broadly sub-quadangular, posterior corners rounded; lateral sclerites of gnathos distinct, medial part with large minutely spined culcitula; tegumen weakly widened anteriorly, with slightly emarginated anterior margin; transtilla sclerotized, longitudinally folded; pedunculus large, sub-triangular, with sclerotized inner edge; valva nearly straight, long, distal part moderately slender, weakly dilated with straight dorsal and ventral edges, apex with two processes, particularly long and pointed dorsal process extended

to posterior third of uncus, slender digitate ventral process at about right-angles to dorsal process; sacculus long, slender, with parallel margins, apically pointed; posterior margin of vinculum deeply incised medially, with pair of short digitate processes, pair of latero-medial processes broadly projected; saccus slightly longer than valva, slender, gradually tapered to apex; phallus long, slender, nearly straight, apically with area of small cornuti.

Female genitalia (Figs 34, 41, 48). Apophysis posterior about four times length of apophysis anterior; segment VIII without processes, smooth; ostium bursae with short lateral folds; apophysis anterior about length of segment VIII; antrum short, about one-fifth length of apophysis anterior, funnel-shaped; posterior part of ductus bursae with pair of long lateral sclerites extending to about apex of apophysis anterior, membranous part of ductus bursae about length of segment VIII including apophysis anterior; signum on right side of entrance to sub-oval corpus bursae, with long and slender crescent-shaped base and long slender hook.

Molecular data. BIN: [BOLD:AAE9478](https://doi.org/10.31233/osf.io/zt9qf). The intraspecific average distance of the barcode region is 0.04%, the maximum distance 0.15% (p-dist) (n = 7). The minimum distance to the nearest neighbor, *C. dianthella*, is 3.05%.

Etymology. The species is named in honour of David Lama (1990–2019), one of the most famous Austrian alpinists, who was tragically killed by an avalanche in Banff National Park (Canada) on the 1st of April 2019. David supported earlier work on landscape conservation in Tyrol with enthusiasm.

Distribution. The species is currently only known from a restricted area in northern Italy (region of Piedmont) and France (Alpes-Maritimes, Alpes-de-Haute-Provence).

Bionomics. Host plant and early stages are unknown but it seems most likely that the species shows a similar behaviour as related taxa with a hostplant restriction to *Dianthus* spp. The adults have been found from late July until late August near rock and scree at altitudes of about 1800 to 2600 m on calcareous soil (Fig. 50), where they were attracted to artificial light sources.

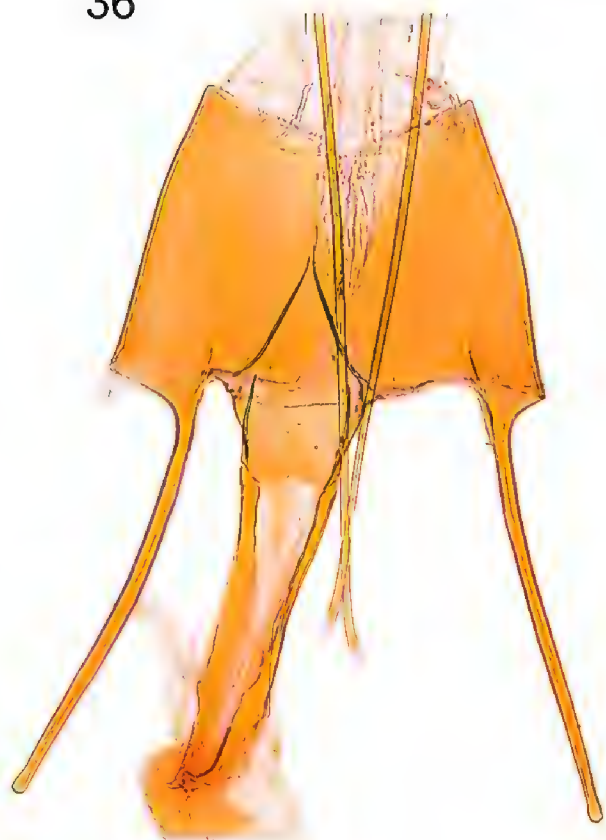
Caryocolum habeleri sp. nov.

<http://zoobank.org/7F0D9CCD-5BD9-4755-ADCE-0D3F21483515>

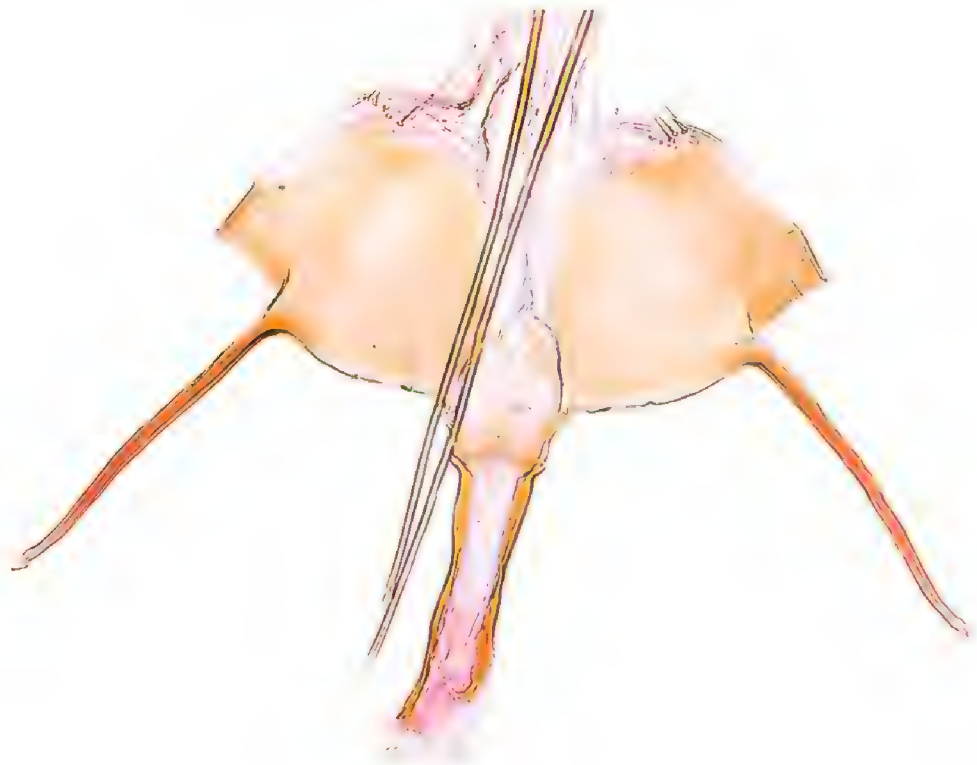
Material examined. **Holotype** ♂, “Laroux – 34 / 13/08/2017 G.Labonne / Grotte de Labeil/Les Siège / 720 m lumières” “Gla-017-2882” “DNA Barcode / TLMF Lep XXX” (TLMF).

Paratypes: France: 1 ♂, same data as holotype, but Gla-017-2883; 1 ♂, Dep. Hérault, Le Caylar, plaine derrière, Gla-016-2821, 25 Aug. 2016, leg. Labonne, gen. slide in glycerin; 1 ♂, Dep. Pyrénées-Orientales, Palau de Cerd., piste forrest. du Camping, 12 Aug. 2016, Gla-016-2606, 12 Aug. 2016, leg. Labonne, gen. slide in glycerin (all RCGL); 1 ♂, Dep. Alpes-Maritimes, Caussols, 1100 m, 7 Sep. 2002, leg. Nel, gen. slide 15062 ♂ J. Nel; 1 ♂, Dep. Alpes-Maritimes, St. Vallier, 6 Sep. 1972, leg.

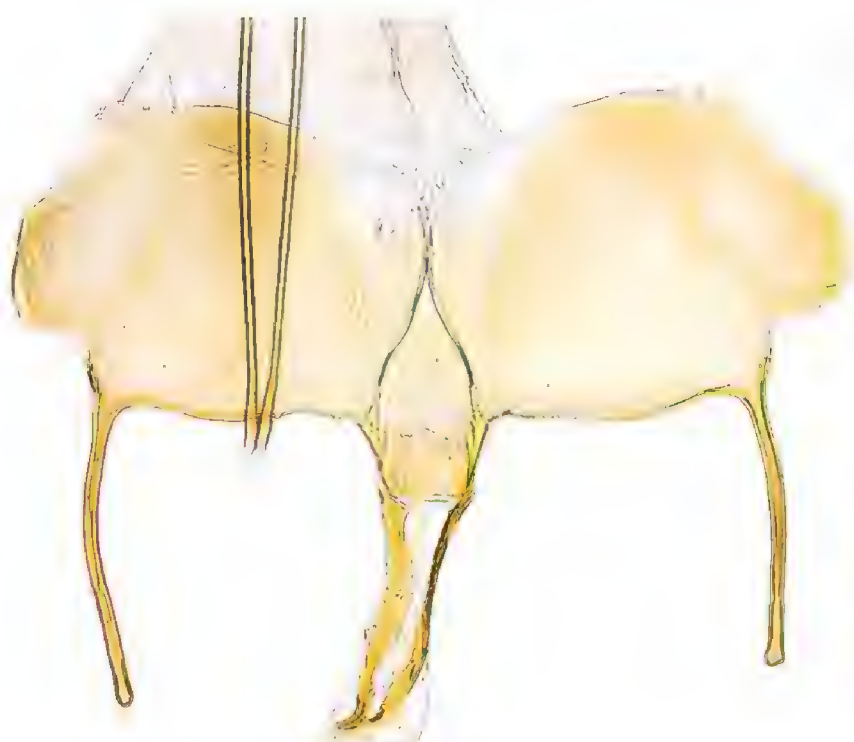
36



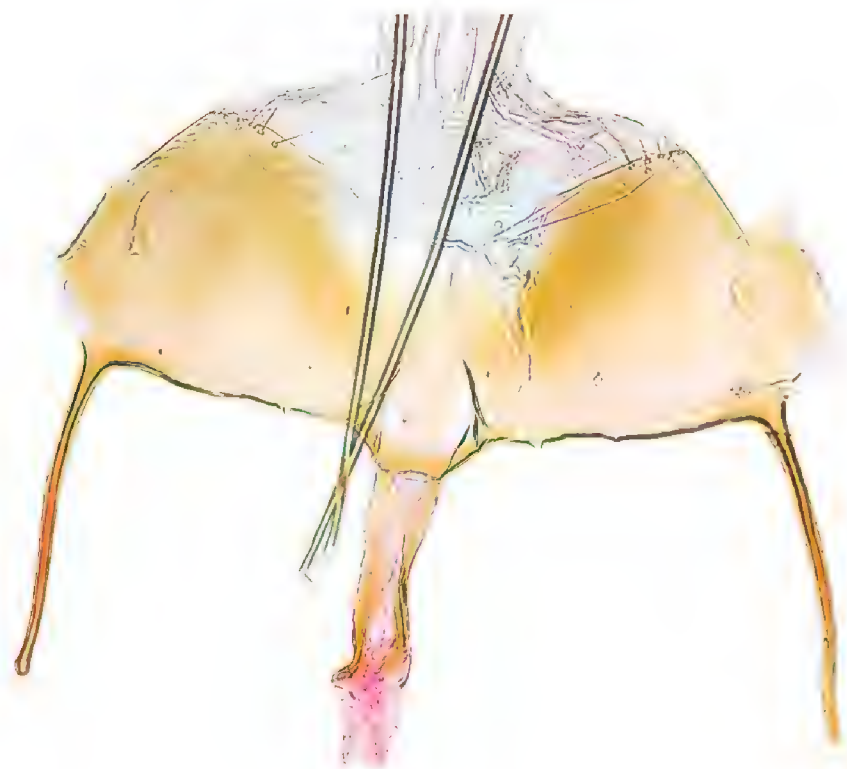
37



38



39



Figures 36–39. Female genitalia (segment VIII). **36** *Caryocolum schleichi*, Syria, slide GU 86/277 P. Huemer; **37** *C. dianthella*, Spain, slide GEL 1285 P. Huemer; **38** *C. improvisella*, Italy, slide GEL 1291 P. Huemer; **39** *C. arenariella*, Sweden, slide GEL 1292 P. Huemer.

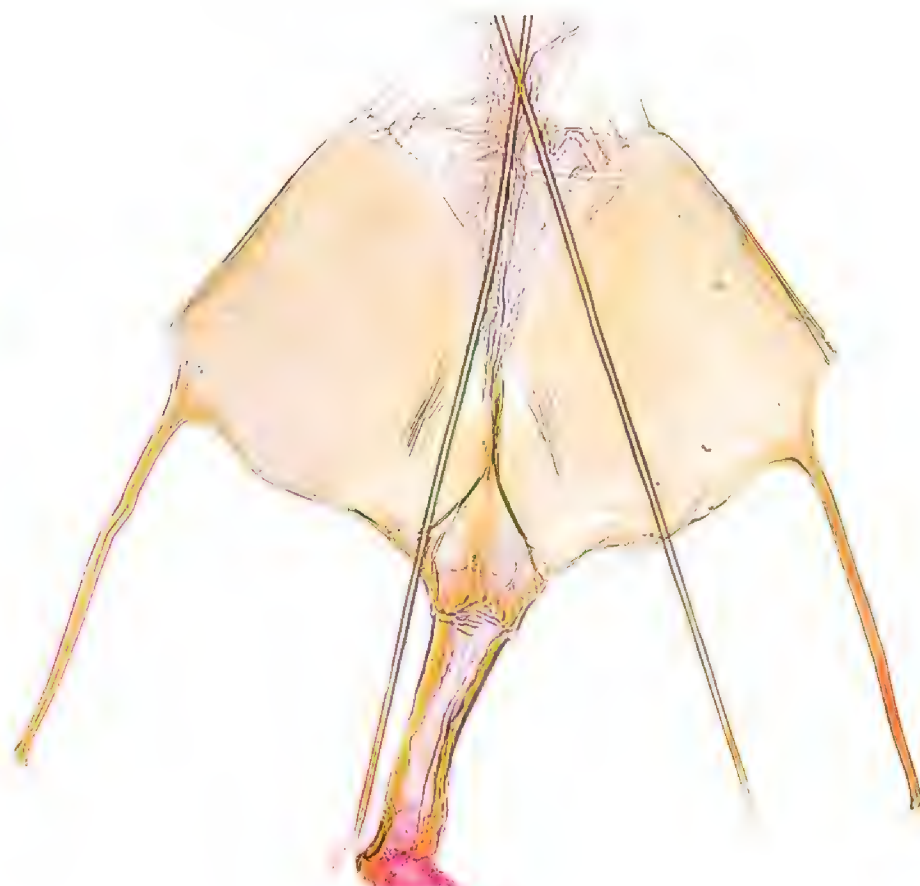
F. Dujardin; 1 ♂, Dep. Alpes-Maritimes, Col de Braus, 1000 m, 23 Aug. 1969, leg. F. Dujardin; 1 ♂, same data, but 28 Aug. 1971, gen. slide GEL 1289 ♂ P. Huemer (all TLMF); 4 ♂♂, 4 ♀♀, Dep. Alpes-Maritimes, Vallon de Cayros, Saorge, Maurion, 718 m, 44°00'06"N, 7°31'08"E, 11 Sep. 2017, leg. Mayr; 1 ♂, same data, but 909 m, 44°00'08"N, 7°31'54"E, 12 Sep. 2019 (all RCTM); 1 ♂, Dep. Vaucluse, Saint-Christol, 11 Aug. 1991, leg. Nel, gen. slide 01472 ♂ J. Nel (TLMF). Ger-

many: 1 ♂, Bayern, Kallmünz, Dallackenrid, 8 Jul. 2002, leg. Lichtmannecker (RCPL); 1 ♂, Bayern, Bissingen, Kesseltal, 24 Aug. 1999, leg. Heindel, gen. slide M1078; 1 ♂, same data, but 28 Jul. 2008, gen. slide M1911; 1 ♀, Bayern, Harburg L., Rollenberg, 28 Jul. 2005, leg. Heindel, gen. slide M1703 (all RCRH); 1 ♂, Bayern, Kelheim, Ihrlenstein "Brannt", 450 m, 16 Jul. 2009, leg. Segerer, DNA Barcode BC ZSM Lep 61823; 1 ♂, Regensburg, Beratzhausen, Laabertal, 21 Jul. 1995, leg. Segerer (all

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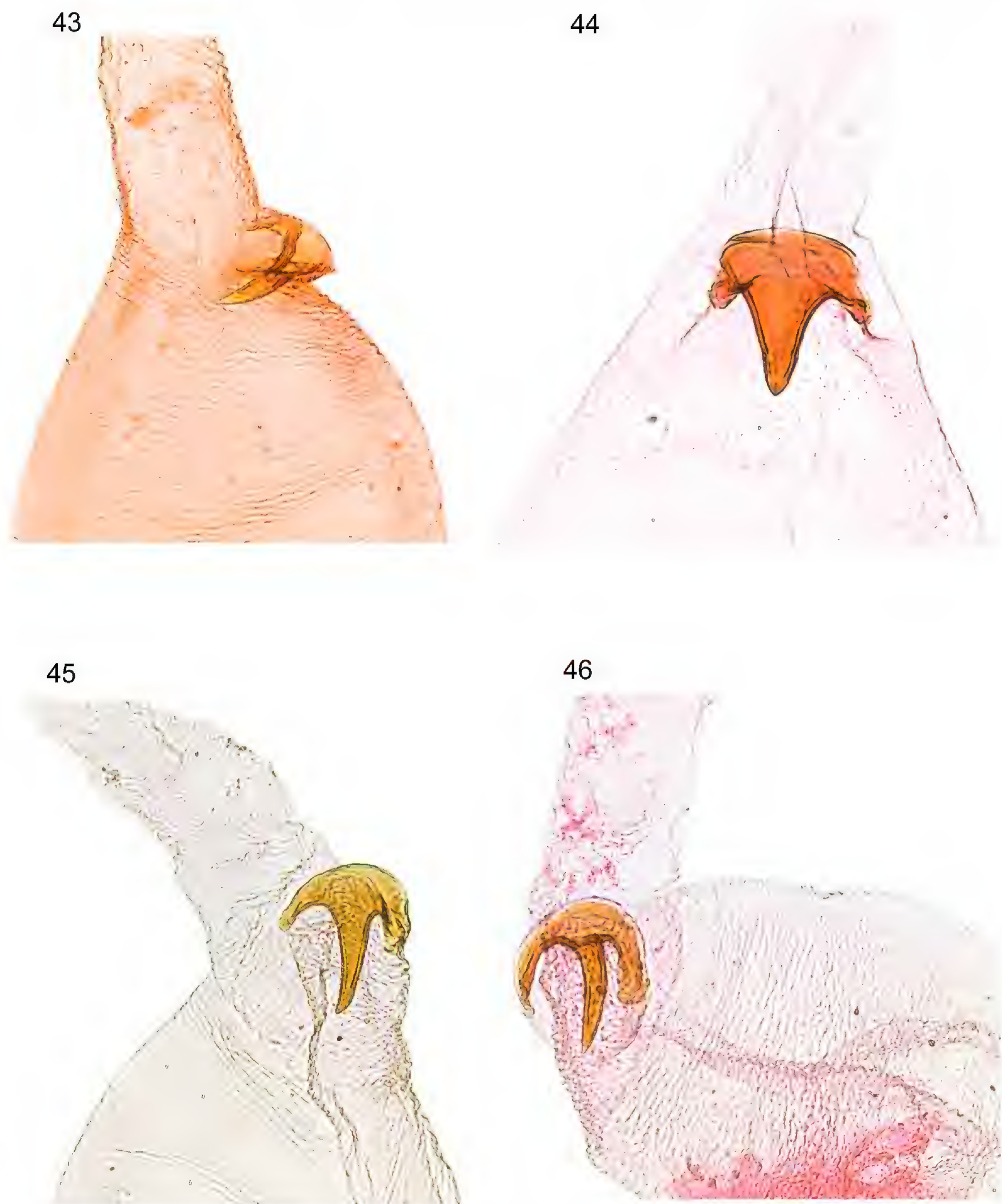
42



Figures 40–42. Female genitalia (segment VIII). **40** *Caryocolum messneri*, paratype, Italy, slide GEL 1295 P. Huemer; **41** *C. lamai*, paratype, Italy, slide GEL 1286 P. Huemer; **42** *C. habeleri*, paratype, Germany, slide M 1703.

ZSM). Switzerland: 1 ♂, Graubünden, Rothenbrunnen, 660 m, 10 Sep. 2004, leg. Schmid, gen. slide without number, DNA Barcode TLMF Lep 21752; 1 ♂, Graubünden, Felsberg, Geissplatte, 730 m, 25 Sep. 2005, leg.

Schmid, gen. slide without number, DNA Barcode TLMF Lep 21751; 1 ♂, Graubünden, Felsberg, 580 m, 28 Aug. 2005, leg. Schmid, gen. slide without number, DNA Barcode TLMF Lep 21750 (all RCJS).



Figures 43–46. Female genitalia (signum). **43** *Caryocolum schleichi*, Syria, slide GU 86/277 P. Huemer; **44** *C. dianthella*, Spain, slide GEL 1285 P. Huemer; **45** *C. improvisella*, Italy, slide GEL 1291 P. Huemer; **46** *C. arenariella*, Sweden, slide GEL 1292 P. Huemer.

Diagnosis. *C. habeleri* differs from *C. schleichi* by the brown rather than white head, thorax and tegulae, it is generally larger than *C. arenariella* and *C. lamai* but otherwise cannot be reliably separated from the other species of the complex from external characters. However, the male genitalia are characterized by the shape of the valva, particularly the short pointed sub-dorsal process and the broad ventral process. A similarly short but broader dorso-apical process is only found

in *C. schleichi* which furthermore has a broader shovel-shaped valva, and in *C. dianthella* with a shorter and dorsally distinctly bulged valva. In all other species of the *C. schleichi* species group, the valva is more slender with a much longer dorso-apical process and smaller dorso-ventral process. The female genitalia are hardly discernible from those of the other species of the *C. schleichi* species group though the moderately long antrum, the distinctly crescent-shaped base of the signum

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Figures 47–49. Female genitalia (signum). **47** *Caryocolum messneri*, paratype, Italy, slide GEL 1295 P. Huemer; **48** *C. lamai*, paratype, Italy, slide GEL 1286 P. Huemer; **49** *C. habeleri*, paratype, Germany, slide M 1703.

in combination with the moderately slender signum hook seem characteristic. However, the individual variation of these characters is insufficiently documented due to lack of material.

Description. Adult (Fig. 12). Forewing length ♂ 4.5–5.5 mm, ♀ 4.0–5.0 mm. Head with dark grey-brown vertex, mottled with white, frons cream-white; first segment of labial palpus dark brown, second segment



Figure 50. Habitat of *Caryocolum lamai*, Italy, Alpi Cozie, Colle Valcavera.

cream-white on inner and upper surface, ventral and outer surface predominantly dark brown, dark brown mixed with few whitish scales on segment three; antenna black, weakly ringed paler. Thorax and tegula dark brown anteriorly, posterior half mixed cream with dark brown and some rusty brown mottling. Abdomen greyish cream on ventral surface. Forewing dark brown, basal half with some rusty-brown mottling, dorsal margin mottled with greyish; white transverse fascia from fold to costa at one-fifth; white medial spot occasionally extended towards costa and dorsal margin; white costal and tornal spots separate; fringes basally dark brown, distal part paler. Hindwing light grey.

Variation. The extension of white marking on the forewing varies considerably and particularly worn specimens look paler.

Male genitalia (Figs 20, 28). Uncus broadly sub-quad-rangular, posterior corners rounded; lateral sclerites of gnathos distinct, medial part with large minutely spined culcitula; tegumen weakly widened anteriorly, with concave, emarginated anterior margin; transtilla sclerotized, longitudinally folded; pedunculus large, sub-triangular, with sclerotized edge; valva nearly straight, oblong, extending beyond middle of uncus, distal part shovel-shaped, apex with two processes, small and short pointed dorsal

and broad digitate ventral process, medially separated weak excavation; sacculus long, knife-shaped; posterior margin of vinculum deeply incised medially, with pair of long digitate processes, pair of latero-medial processes broadly projected; saccus slightly longer than valva, slender, gradually tapered to apex; phallus long, slender, nearly straight, apically with area of small cornuti.

Female genitalia (Figs 35, 42, 49). Apophysis posterior about 4.5 times length of apophysis anterior; segment VIII without processes, smooth; ostium bursae with short lateral folds; apophysis anterior about length of segment VIII; antrum short, about one-quarter length of apophysis anterior, funnel-shaped; posterior part of ductus bursae with pair of long lateral sclerites extending to about apex of apophysis anterior, membranous part of ductus bursae about length of segment VIII including apophysis anterior; signum on right side of entrance to sub-oval corpus bursae, with moderately broad crescent-shaped base and moderately slender hook.

Molecular data. BIN: [BOLD:ACB5067](#). The intraspecific average distance of the barcode region is 0.39%, the maximum distance 0.98% (p-dist) (n = 12). The minimum distance to the nearest neighbor, *C. messneri*, is 3.29%.

Etymology. The species is named in honour of Peter Habeler who, along with Reinhold Messner, completed

the first solo ascent of Mount Everest without supplemental oxygen. Along with the author, Peter is currently involved in the “Blühendes Österreich” conservation foundation. Incidentally, his cousin Heinz Habeler (1933–2017) acquired one of the largest collection of Lepidoptera from the south-eastern Alps, stored at TLMF.

Distribution. The species is currently only known from widely separated localities, ranging from the French Pyrenees to south-eastern Bavaria.

Bionomics. Host-plant and early stages are undescribed but it seems most likely that the species shows a similar behaviour as related taxa with a hostplant restriction to *Dianthus* spp. The adults have been found from late July to late September at artificial light sources near rock and scree on calcareous soil ranging from lower altitudes of the submontane zone up to about 1000 m in the Alps.

Discussion

The *Caryocolum schleichi* species group is an impressive example of the frequently subjective taxonomic assessment of problematic taxa with an allopatric distribution pattern (Mutanen et al. 2012). The different classification of the involved taxa at the species or subspecies level has so far been based solely on morphological features, but the differentiation with molecular methods (Hebert et al. 2003) used here for the first time is a considerable advance. Mutanen et al. (2012) call for at least two mutually independent, diagnostically relevant feature complexes for allopatric taxa in order to arrive at a more objective species delimitation. Divergences in the DNA barcode between the individual taxa of the *Caryocolum schleichi* species group, which were described a considerable time ago, are such an important feature, and independent of morphological discrimination, that supports the species status of the taxa involved. Huemer et al. (2014) from first molecular data had already presumed that named taxa in the *Caryocolum schleichi* species group should be raised to species level, however, without formal implementation of this assumption.

In addition, DNA barcode distances are also an important tool for recognizing possible cryptic diversity. The basic taxonomic structure of the *Caryocolum schleichi* species group – apart from the species or subspecies congestion – was undisputed after the revision of the genus by Huemer (1988). As can now be seen, genetic sequences particularly of alpine populations show a much more complex structure. Instead of the previously postulated species or subspecies *improvisella*, four species are now recognized in the Alps, some with limited distribution (Fig. 50), some with a larger area outside Central Europe. In the area of the Central Alps between Austria, Switzerland and Italy, three species collide spatially and even an occasional sympatric occurrence seems possible. All these taxa could only be morphologically separated after the discovery of genetic distances. Former reports

of the taxon *improvisella* have thus become obsolete and need to be checked thoroughly. The present study shows once again that a broad screening of samples using DNA barcoding can lead to surprises even in Central Europe. Blindly following earlier work must be strongly warned against, even in the case of classic, purely morphologically based revisions.

Acknowledgments

The author is grateful Paul D.N. Hebert and the entire team at the Canadian Centre for DNA Barcoding (Guelph, Canada), whose sequencing work was enabled by funding from Genome Canada through Ontario Genomics, and to the Ontario Ministry of Research and Innovation and NSERC for their support of the BOLD informatics platform. The study was furthermore supported by the Promotion of Educational Policies, University and Research Department of the Autonomous Province of Bolzano – South Tyrol with funds to the projects “Genetische Artabgrenzung ausgewählter arktalpiner und boreomontaner Tiere Südtirols” and “Erstellung einer DNA-Barcode-Bibliothek der Schmetterlinge des zentralen Alpenraumes (Süd-, Nord- und Osttirol)”. The author furthermore thanks Marie-France Leccia (Parc national du Mercantour, Nice) and Michele Ottino (Ente di gestione Aree Protette Alpi Cozie, Salbertrand) for the issuance of the necessary permits. Several colleagues helped with important material and various other support, particularly Richard Heindel (Günzburg, Germany), Ole Karsholt (ZMUC), Gérard Labonne (Montpellier, France), Peter Lichtmannecker (Adlkofen, Germany), Toni Mayr (Feldkirch, Austria), Jacques Nel (La Ciotat, France), Klaus Sattler (NHM), Jürg Schmid (Illanz, Switzerland), and Andreas Segerer (ZSM). Stefan Heim (TLMF) is acknowledged for his kind assistance with photographic work. Robert J. Heckford (Plympton, U.K.) is thanked for his careful language proofreading with valuable comments. Finally useful comments to the manuscript by the subject editor Bernard Landry (Geneva, Switzerland), and the referees Oleksiy Bidzilya (Kiev, Ukraine), Ole Karsholt (Copenhagen, Denmark) and Marko Mutanen (Oulu, Finland) are gratefully acknowledged.

References

- Aarvik L, Bengtsson BÅ, Elven H, Ivinskis P, Jürivete U, Karsholt O, Mutanen M, Savenkov N (2017) Nordic-Baltic Checklist of Lepidoptera. Norwegian Journal of Entomology, Supplement 3: 1–236.
- Agénio R (1962) Resultados científicos de una Pensión de Estudios en el ‘Muséum National d’Histoire Naturelle’ de Paris, con la descripción de un género y otra especie nuevos de lepidópteros españoles, dedicados al Excmo. Sr. D. Jesús Rubio y García-Mina, Ministro de Educación Nacional. Eos. Revista Española de Entomología 38: 147–189. [figs 1–6, pls 2–6]

- Bella S (2008) *Caryocolum siculum* sp. n. (Gelechiidae), feeding on *Gypsophila* (Caryophyllaceae) in Sicily. *Nota lepidopterologica* 31: 69–75.
- Benander P (1926) Über *Lita leucomelanella* Z. und eine dieser nahestehende Art. *Entomologisk Tidskrift* 47: 171–177. [figs 1–16]
- Benander P (1937) Notiser om svenska Microlepidoptera, med beskrivning av *Lita arenariella* n. sp. *Opuscula Entomologica* 2: 29–32. [figs 1–2]
- Burmann K (1990) Beiträge zur Microlepidopteren-Fauna Tirols. XIV. *Caryocolum* Gregor & Povolný, 1954 (Insecta: Lepidoptera, Gelechiidae). *Berichte des naturwissenschaftlich-medizinischen Vereins Innsbruck* 77: 171–184.
- Chrétien P (1925) La légende de *Graellsia isabellae*. Appendice. *L'Amateur de Papillons* 2: 241–247.
- Christoph H (1872) Neue Lepidoptera des europaischen Faunengebietes. *Horae Societatis Entomologicae Rossicae* 9: 3–39.
- Derra G (1985) *Caryocolum hackeri* sp. n., eine neue Gelechiidae aus den Pyrenäen Frankreichs und Spaniens (Lepidoptera, Gelechiidae). *Entomofauna, Linz* 6: 373–379.
- deWaard JR, Ivanova NV, Hajibabaei M, Hebert PDN (2008) Assembling DNA Barcodes: Analytical Protocols. In: Martin CC (Ed.) *Methods in Molecular Biology: Environmental Genomics*. Humana Press Inc., Totowa, 364 pp. [275–293] https://doi.org/10.1007/978-1-59745-548-0_15
- Grange J-C, Nel J (2012) *Caryocolum dauphini* n. sp., un endémique du Sud-Ouest alpin découvert dans le Parc national du Mercantour (Lep. Gelechiidae, Gnorimoschemini). *Oreina* 17: 24–25.
- Gregor F, Povolný D (1954) Systematische und zoogeographische Studie über die Gruppe der Arten *Gnorimoschema* Busck mit Rücksicht auf die richtige Diagnostik des Schädling *Gnorimoschema ocellatellum* Boyd. *Zoologické a Entomologické Listy* 3: 83–97. [pl. 7, map.]
- Hebert PDN, Cywinska A, Ball SL, deWaard JR (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society Biological Sciences Series B* 270: 313–321. <https://doi.org/10.1098/rspb.2002.2218>
- Huemer P (1987) Eine modifizierte Genitalpräparationstechnik für die Gattung *Caryocolum*. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 60: 207–211.
- Huemer P (1988) A taxonomic revision of *Caryocolum* (Lepidoptera: Gelechiidae). *Bulletin of the British Museum of Natural History (Entomology)* 57: 439–571.
- Huemer P, Karsholt O (2010) Gelechiidae II (Gelechiinae: Gnorimoschemini). In: Huemer P, Karsholt O, Nuss M (Eds) *Microlepidoptera of Europe* (Vol. 6). Apollo Books, Stenstrup, 586 pp. https://doi.org/10.1163/9789004260986_002
- Huemer P, Karsholt O (2020) Commented checklist of European Gelechiidae (Lepidoptera). *ZooKeys* 921: 65–140. <https://doi.org/10.3897/zookeys.921.49197>
- Huemer P, Karsholt O, Mutanen M (2014) DNA barcoding as a screening tool for cryptic diversity: an example from *Caryocolum*, with description of a new species (Lepidoptera, Gelechiidae). *ZooKeys* 404: 91–111. <https://doi.org/10.3897/zookeys.404.7234>
- Huemer P, Nel J (2005) *Caryocolum mazeli* sp. n., a new species from southern France (Lepidoptera, Gelechiidae). *Bulletin de la Société entomologique de France* 110: 125–127.
- Klimesch J (1953–1954) Die an Caryophyllaceen lebenden europäischen *Gnorimoschema* Busck (= *Phthorimaea* Meyr.)-Arten. *Zeitschrift der Wiener Entomologischen Gesellschaft* 38 (1953): 225–239. [272–282, 311–319; 39 (1954): 273–288, 335–341, 357–362]
- Klimesch J (1968) Die Lepidopterenfauna Mazedoniens IV. Microlepidoptera. *Posebno Izdanje Prirodonaucen Muzei Skopje* 5: 1–201. [figs 1–10]
- Mutanen M, Hausmann A, Hebert P, Landry J-F, de Waard J, Huemer P (2012) Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in Arctic-Alpine Lepidoptera. *PLoS ONE* 7: e47214. <https://doi.org/10.1371/journal.pone.0047214>
- Nel J, Requena E (2017) Description d'une nouvelle espèce du groupe de *Caryocolum amaurella* (Hering, 1924), découverte dans les Pyrénées: *C. tredosella* sp. n. (Lepidoptera, Gelechiidae). *Revue de l'Association Roussillonnaise d'Entomologie* 26: 177–179.
- Pitkin LM (1986) A technique for the preparation of complex male genitalia in Microlepidoptera. *Entomologist's Gazette* 37: 173–179.
- Povolný D (1977) Drei neue Arten der Tribus Gnorimoschemini (Lepidoptera, Gelechiidae) aus dem westpaläarktischen Eremialgürtel. *Acta Universitatis Agriculturae, Brno (A)* 25(4): 169–175.
- Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Molecular Ecology Notes* 7: 355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- Rebel H (1936) Drei neue Mikrolepidopterenarten aus der Schweiz. *Zeitschrift des Österreichischen Entomologen-Vereins, Wien* 21: 2–4.
- Robinson GS (1976) The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. *Entomologist's Gazette* 27: 127–132.
- Tamura K, Stecher G, Peterson D, Filipowski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. <https://doi.org/10.1093/molbev/mst197>
- Zeller PC (1839) Versuch einer naturgemäßen Eintheilung der Schaben. *Isis, Leipzig* 1839: 167–220.